BioControl
DOI 10.1007/s10526-017-9805-0

Life history of the harlequin ladybird, *Harmonia axyridis*: a global meta-analysis

C. Lidwien Raak-van den Berg · Lia Hemerik · Wopke van der Werf · Peter W. de Jong · Joop C. van Lenteren

Received: 25 February 2016 / Accepted: 23 March 2017

Abstract The harlequin ladybird, *Harmonia axyridis,* is an important natural enemy of aphids throughout the world, but is now also considered an invasive alien species. We performed a meta-analysis of published life history data to address the question whether invading populations in Europe and North America have life history parameters that differ from native populations in Asia, explaining the beetle's invasion success in new territories. In this meta-analysis, we accounted for important covariables that are often reported in published studies such as temperature, food source (aphids or eggs of *Ephestia kuehniella*), strain (laboratory or field populations) and photoperiod. Temperature was a key factor having consistent large effects on development rate, survival and reproductive characteristics of *H. axyridis*. Food source, strain, and photoperiod had effects on some, but not all characteristics, and their overall effect across characteristics was minor. Individuals of invasive populations had a shorter pre-oviposition period and higher fecundity at low temperatures than those of native populations, and a greater longevity across all temperatures. No differences in survival were found between native and invasive populations, while differences in development rate were not consistent, with opposing results obtained according to the way development rate was measured in trials reported in the literature. Results of this meta-analysis support the hypothesis that the life history of the beetle has changed during its invasion into North America and Europe. Invasive populations had a shorter pre-oviposition period and higher fecundity at low temperatures, as well as a greater longevity across all temperatures than native populations. These differences may partially explain the invasive success of *H. axyridis*.

Handling Editor: Peter Brown.

Electronic supplementary material The online version of this article (doi:10.1007/s10526-017-9805-0) contains supplementary material, which is available to authorized users.

C. L. Raak-van den Berg (✉) · P. W. de Jong · J. C. van Lenteren
Laboratory of Entomology, Wageningen University, PO Box 16, 6700AA Wageningen, The Netherlands
e-mail: LidwienRaakvandenBerg@gmail.com

C. L. Raak-van den Berg
Netherlands Food and Consumer Product Safety Authority, National Plant Protection Organization, PO Box 9102, 6700 HC Wageningen, The Netherlands

L. Hemerik
Biometris, Wageningen University, PO Box 16, 6700 AA Wageningen, The Netherlands

W. van der Werf
Plant Sciences, Crop & Weed Ecology Group, Wageningen University, PO Box 430, 6700 AK Wageningen, The Netherlands

Published online: 05 April 2017

Keywords Meta-analysis · Invasive populations · *Harmonia axyridis* · Life history characteristics · Temperature dependence · Native area · Coccinellid

Introduction

The harlequin ladybird *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) was introduced to various areas of the world as a biological control agent of aphids. It was taken to the USA in 1916 and numerous releases followed, with the first established population recorded in 1988 (Chapin and Brou 1991). Introduction into Europe took place in 1982 and the first established population was found in 2000–2001 (Brown et al. 2011). In autumn 2002 it was recorded in the field in the Netherlands (Cuppen et al. 2004) and by 2006 it had spread throughout the country (Brown et al. 2008). The species is now established in 40 countries in Europe, three countries in North America, most countries in South America and four countries in Africa (Brown 2013; Roy et al. 2016).

After initial enthusiasm about the effectiveness of *H. axyridis* as a biological control agent, concern has risen on its side effects. First of all, there is worry about competitive displacement of native ladybirds (Evans et al. 2011). Secondly, the beetles cause damage when feeding on soft fruit (e.g. grapes; Kögel 2012) and on flowers of cultivated fruit (e.g. date; Li et al. 1992). Thirdly, the beetle is considered a nuisance due to its aggregation in and around homes for overwintering (Wang et al. 2011) and people may develop allergies (Goetz 2008). Because of these negative impacts, the beetle is currently considered an invasive alien species (Brown et al. 2011) and is no longer commercially available in most of Europe (van Lenteren 2012).

The invasion of *H. axyridis* has stimulated research on its natural history, and many reviews have appeared on various aspects of ecological relationships, its invasion process and negative impacts. A major issue is the effect of its establishment on native ladybirds and other non-target organisms (Majerus et al. 2006). Its invasion history and quick spread over Europe were discussed in several papers (e.g. Brown et al. 2008; Poutsma et al. 2008). Its dominance in intraguild predation, possibly resulting in a decrease of populations of native ladybirds, has received much attention (e.g. Pell et al. 2008). Also, the limited effect of European natural enemies in reducing *H. axyridis* populations (Raak-van den Berg et al. 2014; Roy et al. 2011) and methods of managing this invasive species have been considered (Kenis et al. 2008).

A question that has not received much attention in these reviews is whether invasive *H. axyridis* have a different life history compared with those in the area of origin (but see Sloggett 2012). Rapid evolutionary changes during invasion are common in plant and animal species (e.g. Whitney and Gabler 2008). Changes in life history characteristics of the beetle may have contributed to the invasive success of the species. Variation in life history characteristics between coccinellid populations from different geographic origins has indeed been found in some studies (e.g. Obrycki and Tauber 1982), but not in others (e.g. Phoofolo and Obrycki 1995). Differences between invasive and native populations of *H. axyridis* might be explained by the following mechanisms: (1) sampling effect: a non-random sample with a strong temperature response is the source of the invasive populations; (2) admixture of two geographically distinct native populations (Blekhman et al. 2010; Lombaert et al. 2011), which in turn have admixed with the European biocontrol strain (Lombaert et al. 2010); (3) purging of deleterious alleles at the bottleneck of the invasive process (Facon et al. 2011); and (4) captivity rearing, stimulating fast development and high fecundity, which has changed the biocontrol strains that have been introduced (Tayeh et al. 2012).

A quantitative analysis of data is needed to establish whether native and invasive populations of the beetle do differ in life history characteristics. We conducted a meta-analysis on life history characteristics data of *H. axyridis.* Meta-analysis examines the results from multiple studies to synthesize findings in a quantitative manner and increases the statistical power by combining data (Glass 1976). In meta-analyses data are not filtered by the personal views of the researcher and these are, therefore, regarded as a more objective way of synthesizing information from the literature than narrative reviews (Koricheva et al. 2013). Here we use meta-analysis to combine results of studies on the life history of *H. axyridis* in order to test the hypothesis that life history characteristics of isolates of *H. axyridis* in the invasive range (e.g. America, Europe) differ from those in the native range (Asia). In

order to raise the sensitivity of this analysis we consider covariables that are likely to affect life history characteristics: temperature, food source, whether the beetle had been cultured for a long time under laboratory conditions, and photoperiod during the experiments. Because insects are poikilothermic we expect that temperature influences all life history variables for development, survival, pre-oviposition period, generation time and daily fecundity (Logan et al. 1976).

We use model selection to identify the most satisfactory model and ask what is the best model explaining each life history characteristic, and what are statistically equivalent models. We then interpret the outcomes to answer our main questions: do life history characteristics of *H. axyridis* differ between the invasive and native range and can these differences explain its invasion success?

Methods

Data collection

Studies from 1900 onwards on life history characteristics of *H. axyridis* were gathered by literature searches in CAB abstracts, ISI Web of Science, Biological records, Zoological records, and Agricola, using the search term '*Harmonia axyridis*' in the search fields for title, abstract, text, and keywords. Further references were found by checking bibliographies of the retrieved papers and previously published reviews. The last search was conducted in July 2016. Papers were selected that contained original empirical data on life history characteristics (Table 1). Four inclusion criteria were used: (1) conducted under biologically relevant temperatures (14–35 °C), (2) with unlimited supply of aphids or *Ephestia kuehniella* Zeller (Lepidoptera, Pyralidae) as food, (3) conducted during summer; and (4) using normal, winged beetle genotypes. A total of 82 publications (listed in Supplementary Information 1) met the inclusion criteria. Further details on data collection and methods are given in Supplementary Information 2. Raw data are available at http://dx.doi.org/10.17026/dans-zt7-dhb6.

The key life history characteristics for any organism are development rate, survival and reproduction (Caswell 2001), but there are many different ways in which these may be measured, e.g. for separate larval instars or for the larval stage as a whole. To accommodate differences between studies, we use in our analyses 22 different life history characteristics as response variables. Both development rate and fraction survival over the whole duration of a stage were defined as response variables for nine developmental stages: (1) egg, (2) L1, (3) L2, (4) L3, (5) L4, (6) pupa, (7) larva, (8) 'larva plus pupae', and (9) total immature stage. Four life history characteristics were considered for the adult: pre-oviposition period, longevity, generation time and daily fecundity.

Table 1 Overview of the data (number of studies and number of data points) from the literature search

Response variable	Studies	Data points (# individuals)
Development		
Egg	18	50 (8268)
Larva 1	28	73 (6338)
Larva 2	31	79 (5940)
Larva 3	31	80 (5999)
Larva 4	32	84 (6432)
Larva	43	142 (7975)
Pupa	29	84 (6385)
Larva + pupa	40	112 (8552)
Immature stages	23	82 (9544)
Survival		
Egg	29	92 (269,118)
Larva 1	10	20 (2677)
Larva 2	9	22 (2609)
Larva 3	11	23 (27,710)
Larva 4	11	24 (2673)
Pupa	13	23 (2726)
Larva	13	34 (3662)
Larva + pupa	23	38 (3471)
Immature stages	9	27 (6720)
Adult		
Pre-oviposition period	29	85 (4245)
Generation time	13	56 (3828)
Fecundity	33	72 (2668)
Longevity	16	42 (3081)

The third column shows the total number of data points available for each response variable with between brackets the total number of individuals on which these data points are based

Data processing

Durations of the development stages were converted to rates of development by taking the reciprocal: DVR = 1/duration (De Wit and Goudriaan 1978). The same was done for the pre-oviposition period and the total generation time reported in publications. Survival was defined as the fraction surviving a stage or a sequence of stages. Daily fecundity was calculated as the average number of eggs laid per day over a defined period. Factors or factor levels were excluded from analysis if too few data were available and factors were merged if this was necessary to avoid strongly unbalanced designs (e.g. due to empty cells, see Supplementary Information 2 and Supplementary Information 3 for details).

Model fitting and model selection

All statistical models were fitted to the data as linear mixed effects models using the function lmer from the R package lme4 (Bates et al. 2015). 'Study' was modelled as a random effect, to account for differences between studies that are not accounted for by fixed effects of the five categorical variables included in the model (Zuur et al. 2009). First, the most complex model was constructed for each response variable. Then, all possible less complex models that could be assembled with the factors of the most complex model, were fitted to the data using the R function dredge from the R package MuMIn for multi-model inference (Barton 2014, R version 3.0.2). Data records were weighted according to the square root of the number of individuals used to measure the life history characteristic.

In the fitted models, temperature was included as a continuous variable, as it was reported in all studies and it is well established that life history characteristics of insects are determined by temperature (e.g. De Wit and Goudriaan 1978; Logan et al. 1976). Furthermore, four categorical variables were included: geographic origin (O: native (Asian) or invasive), photoperiod (P: 14 h light, 16 h light, or natural daylight, i.e. no artificial control of photoperiod), food (F: aphid or *Ephestia*), and strain (S: laboratory reared or wild i.e. field-collected not more than four generations ago). In analyses of longevity we also included the categorical variable 'sex' (G).

Development rates (including the rates of pre-oviposition period and generation time) were fitted as linear functions of temperature and covariables. Daily fecundity was fitted with a parabolic function of temperature. In the full models (with most factors included) for the eleven development rates, longevity and fecundity, each factor and its interaction with temperature was at least included. The first-order interactions were included in the order O × P, O × F, O × S, O × G, P × F, P × S, P × G, F × S, F × G, S × G, as long as the model could be fitted (i.e. no singular model matrix resulted during estimation). The models for survival included higher powers of the temperature up to the fourth power to account for non-linear relationships. For survival of the single stages the factor strain and the combined factor origin-photoperiod were included along with their interaction with temperature. Survival of the egg, larva, 'larva plus pupa' and all immature stages had a most complex model with all or almost all combinations of origin, photoperiod, food and strain and their interaction with temperature. Here, the first-order interactions were included in the order O × P, O × F, O × S, P × F, P × S, F × S, as long as the model could be fitted.

The best models were selected using Akaike's Information Criterion corrected for small sample size (Bolker 2008). The 'best model' or, equivalently, most supported model is characterized by the lowest AICc value among the 'set of most supported models' i.e. the set of models within the interval $\Delta AICc < 2$ that are considered equivalent (Hilborn and Mangel 1997). We used Ockham's razor (principle of parsimony) to choose within this set of most supported models, the 'most parsimonious model' i.e. the model with the least number of parameters. These models are shown in Figs. 1, 2 and 3. An overview of the 20 best models for each life history characteristic is available at http://dx.doi.org/10.17026/dans-zt7-dhb6.

Overview of life history parameters for native and invasive *H. axyridis* populations

To enable a comparison between native and invasive populations, we constructed a summary overview of different life history parameters as a function of temperature. Life history parameters were predicted for 15, 20, 25 and 30 °C, using for predicting the 'set

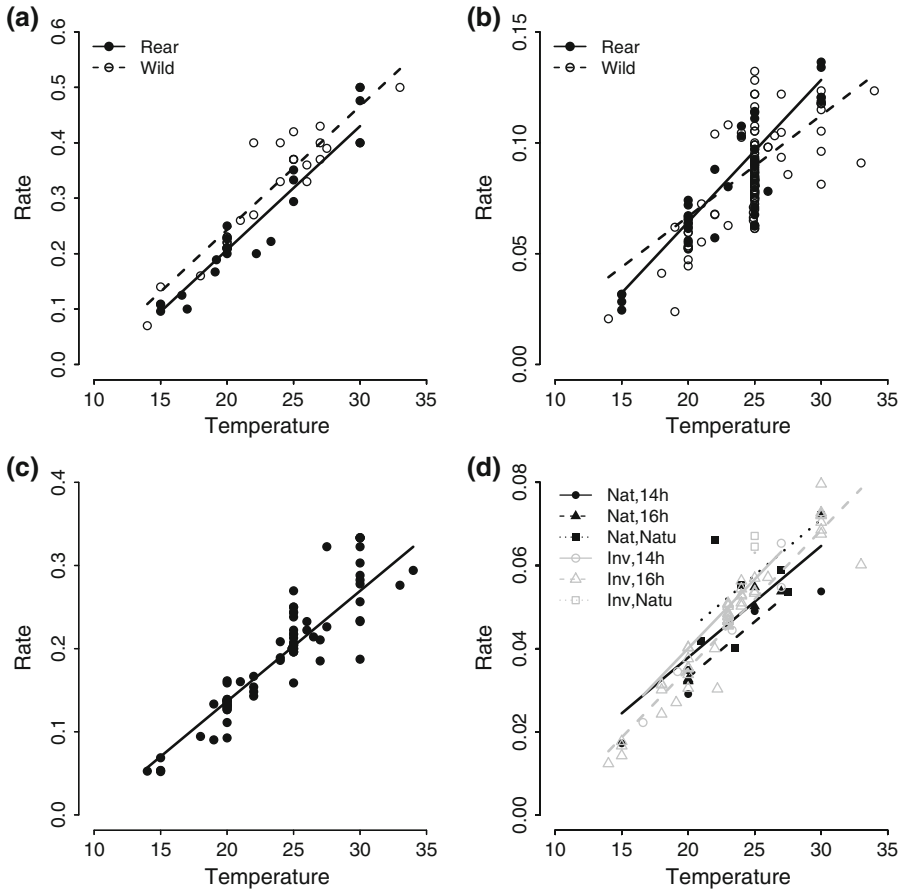

Fig. 1 Development rate of **a** egg, **b** larva, **c** pupa, and **d** immature stages of *H. axyridis*. Data points from literature are represented by *symbols*. Fitted relationships of the most parsimonious model are represented by *lines* that are only shown when data are available for that set of factors. *Legends* show the combination of factors. Geographic origin: native (Nat) or invasive (Inv). Photoperiod: short (14 h), long (16 h), or natural (Natu). Strain: wild or reared

of best origin models' consisting of either: (1) the most parsimonious model, or (2) the best model (with lowest AICc) that contained origin as a fixed factor. The latter was done if the most parsimonious model did not contain origin and a model with origin as a factor was within the set of most supported models. Two predictions of each life history characteristic are given: for native populations and for invasive populations. A single prediction was given if the set of most supported models did not include a model with origin as an explanatory variable. The predicted life history characteristics at different temperatures were calculated for wild, aphid-fed populations under long-day conditions if these factors were included in the most parsimonious or best origin model.

Results

Temperature had a large and consistent influence on all life history parameters. Therefore all fitted models are shown as functions of temperature with other selected variables as categorical covariables modifying the relationship to temperature. Fitted lines in these figures may not go through the centre of gravity of the data. This is a common phenomenon with mixed effects models resulting from the unequal weighting of different points in relation to sample size and the nested data structure resulting from experiments being nested within publications. Below, a description is given of the most parsimonious models for each of the 22 life history characteristics. In 15 out of 24 cases, a 'best origin model' was included in the set of most supported models, but not in the nine other cases, indicating that the explanatory value of origin was too small to justify its inclusion in the model.

Models for development rate

All models for development rate show a linear increase of development rate with temperature.

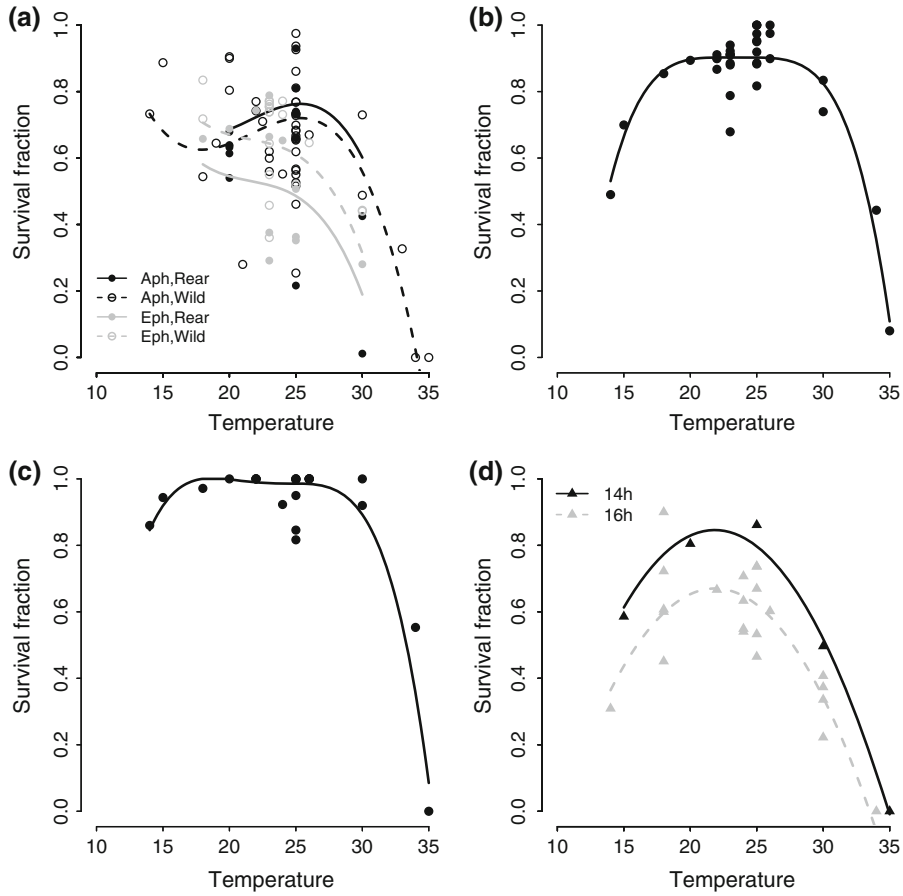

Fig. 2 Survival of **a** egg, **b** larva, **c** pupa, and **d** immature stages of *H. axyridis*. Data points from literature are represented by *symbols*. Fitted relationships of the most parsimonious model, are represented by *curves* that are only shown when data are available for that set of factors. *Legends* show the combination of factors. Photoperiod: short (14 h) or long (16 h). Food: aphid (Aph) or *Ephestia* (Eph). Strain: wild or reared

Development rate of the egg stage

Eggs from wild populations developed faster than eggs from reared populations across all temperatures (Fig. 1a). Strain was the only factor modulating the temperature effect.

Development rate of the larval stage

Reared populations during larval development responded more strongly to temperature increase than wild populations (Fig. 1b). However, the most parsimonious models for separate larval stages included photoperiod (L1) or geographic origin (L2–L4) in addition to temperature (Supplementary Information 3).

Development rate of the pupal stage

The most parsimonious model for pupal development (Fig. 1c) only contained a response to temperature.

Development rate of the larval plus pupal stages

Development during larval plus pupal stages showed a stronger response to temperature for reared than for wild populations, similar to the model for larval development. For both reared and wild populations, development was faster under short-day conditions than under long-day conditions.

Development rate of the egg plus larval plus pupal stages

Immature development rate increased with temperature. Invasive populations responded more strongly to temperature than native populations, with invasives developing faster at high temperatures than natives at the same photoperiod. In both native and invasive populations, development was faster under short-day than under long-day conditions. In native populations, development was fastest under natural-day conditions (Fig. 1d).

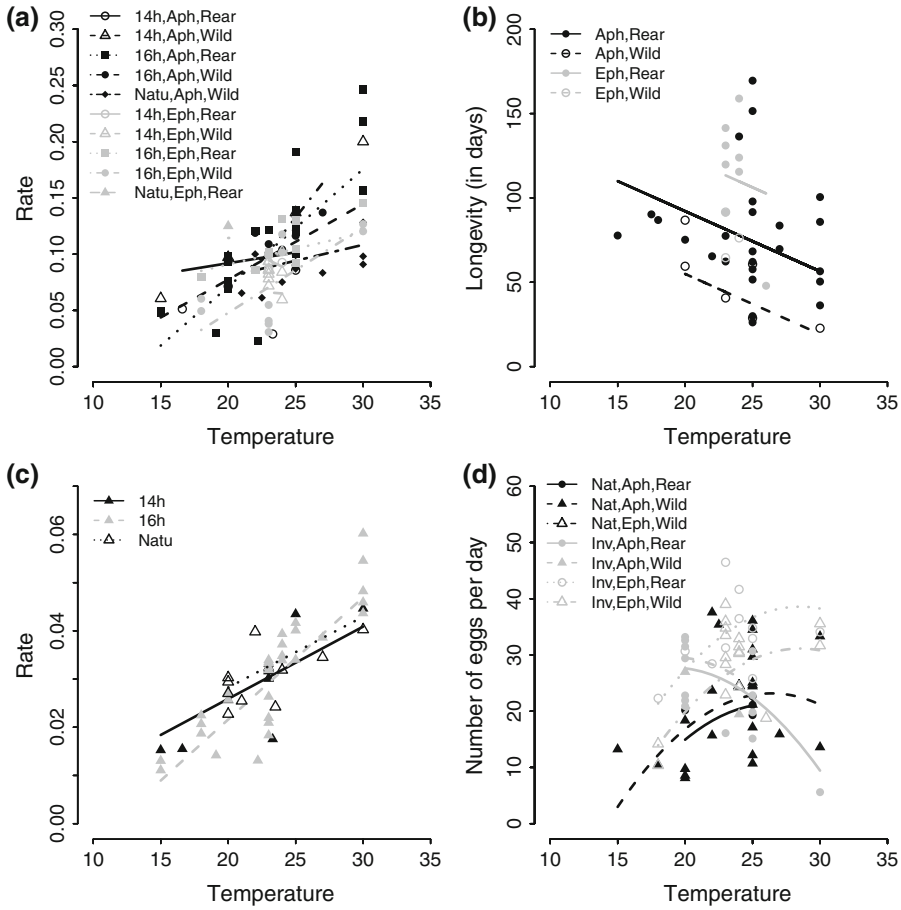

Fig. 3 Adult parameters of *H. axyridis* **a** 1/pre-oviposition period, **b** longevity, **c** 1/generation time, and **d** daily fecundity. Data points from literature are represented by *symbols*. Fitted relationships of the most parsimonious model are represented by *lines* (**a**, **b**, and **c**) and *curves* (**d**) that are only shown when data are available for that set of factors. Legends show the combination of factors. Geographic origin: Native (Nat) or invasive (Inv). Photoperiod: short (14 h), long (16 h), or natural (Natu). Food: aphid (Aph) or *Ephestia* (Eph). Strain: wild or reared

Models for survival

Temperature had a strong effect on survival and this effect was best described with a polynomial of an order between two and four. The resulting responses to temperature were optimum curves with a plateau or optimum in the range of 20–30 °C (Fig. 2). Survival of most stages decreased to zero at temperatures around 35 °C. There was still survival at 14 °C, but due to lack of data below 14 °C a lower threshold temperature could not be assessed.

A majority of the most parsimonious models contained temperature as the single explanatory variable. Exceptions were the models for the egg stage (food and strain as additional variables), L3 (photoperiod and origin as additional variables) and immature survival (photoperiod as additional variable).

Survival during the egg stage

The survival of eggs laid by reared populations of *H. axyridis* was substantially higher when ladybirds were fed on aphid food rather than *Ephestia*, while this difference was present but smaller for *H. axyridis* populations collected in the wild (Fig. 2a).

Survival during the larval stages

Survival in the larval instars was a function of temperature only, with a maximum fraction survival of 0.903 at 23.5 °C and a broad range of temperatures (20–27 °C) for which the fraction survival was above 0.89 (Fig. 2b).

Survival during the pupal stage

Survival of the pupal stage was a function of temperature only, with a plateau at a fraction survival of 1.00 at temperatures from 17.5 to 19.2 °C. For a broad range of temperatures (16–28 °C) fraction survival was above 0.96 (Fig. 2c).

Survival of the entire immature life stage (egg-pupa)

Survival of the entire immature stage (egg-pupa) was higher (but few data) under short-day conditions (14 h) as compared to long-day conditions (16 h). The highest fraction survival under short-day conditions was 0.85 and under long-day conditions 0.67, both at 22 °C. At both short and long day length, 0.9 or more of the maximum survival was reached between 18.5 and 25.5 °C (Fig. 2d).

Models for the adult stage

Pre-oviposition period

In addition to temperature, the most parsimonious model for pre-oviposition development included all explanatory variables, except geographic origin (Fig. 3a). Results should be interpreted with caution because of the potential of collinearity between explanatory factors.

Longevity

Most of the non-hibernating adults of *H. axyridis* have longevities between 22 and 100 days. Longevity (Fig. 3b) decreased with temperature. Average longevity was longest for wild, *Ephestia*-fed populations (124 days at 20 °C), shorter for wild, aphid-fed (92 days at 20 °C) and reared *Ephestia*-fed populations (87 days at 20 °C), and shortest for reared aphid-fed populations (56 days at 20 °C). For *Ephestia*-fed populations only data in a small temperature range were available, which hinders a robust comparison with aphid-fed populations. The most parsimonious model did not contain an effect of geographic origin, sex, photoperiod, or food.

Generation time

The rate at which generations follow each other (calculated as the inverse of generation time; Fig. 3c) increased with temperature. The response to temperature was stronger under long-day than under short or natural-day conditions.

Reproduction

Fecundity was highest for *Ephestia*-fed, invasive populations: 38.5 eggs per day at 29 °C. Lowest fecundity was found for native populations. The fitted model indicates that aphid-fed, invasive populations have a lower optimum temperature for fecundity (28 eggs per day at 19 °C) than the invasive populations that are fed on *Ephestia* or than native populations (Fig. 3d).

Effects of origin of *H. axyridis* on life history parameters

Analysis of the effect of geographic origin in the set of 'best origin models' gave contradictory results for development rate (Table 2). On the one hand, the pre-adult development (from egg to adult eclosion) was at all temperatures shorter for the invasive populations than for native populations. On the other hand, models for the development of some of the single stages of invasive populations, except the egg stage, as well as for all larval stages together and for larval plus pupal stages, indicated that development takes longer for the invasive populations. Therefore, the literature points to differences between invasive and native populations, but an analysis of separate stages gives a different outcome and conclusion than an analysis of the rate of development through all the pre-adult stages taken together.

Regarding survival, the overall outcome of the meta-analysis is a lack of effect of geographic origin, or a small effect. Substantial effects of geographic origin were found in the adult stage. The pre-oviposition period at lower temperatures was shorter in invasive populations, longevity of invasive populations tended to be longer than that of natives across all temperatures, and invasive populations had at

Table 2 Estimated values of life history parameters (SE) for wild, aphid-fed native and invasive populations of *H. axyridis* under long-day conditions based on the 'best origin model'

	Temperature		15 °C		20 °C		25 °C		30 °C	
		#20	Native	Invasive	Native	Invasive	Native	Invasive	Native	Invasive
Development time (days)	Egg	12	7.57 (0.68)	9.93 (1.04)	4.08 (0.15)	4.68 (0.19)	2.80 (0.06)	3.07 (0.08)	2.13 (0.04)	2.28 (0.06)
Development time (days)	Larva 1	9	*6.84 (1.11)*	*5.85 (0.82)*	*3.53 (0.24)*	*3.25 (0.21)*	*2.38 (0.10)*	*2.24 (0.10)*	*1.79 (0.07)*	*1.72 (0.06)*
Development time (days)	Larva 2	17	3.22 (0.44)	5.28 (1.35)	2.24 (0.18)	2.59 (0.30)	1.72 (0.10)	1.72 (0.13)	*1.39 (0.07)*	*1.28 (0.08)*
Development time (days)	Larva 3	17	4.01 (0.59)	6.64 (1.68)	2.80 (0.22)	3.06 (0.30)	*2.15 (0.11)*	*1.99 (0.12)*	*1.75 (0.09)*	*1.47 (0.07)*
Development time (days)	Larva 4	14	7.55 (0.72)	11.38 (1.81)	5.63 (0.34)	6.67 (0.55)	4.49 (0.20)	4.72 (0.27)	*3.73 (0.15)*	*3.65 (0.17)*
Development time (days)	Pupa	8	***14.25 (1.29)***		***7.32 (0.27)***		***4.93 (0.12)***		***3.71 (0.08)***	
Development time (days)	Larva	13	24.78 (2.98)	29.73 (5.18)	15.46 (0.97)	17.25 (1.52)	11.24 (0.48)	12.15 (0.71)	8.82 (0.33)	9.38 (0.45)
Development time (days)	Larva + Pupa	9	***35.94 (3.00)***		***22.42 (0.99)***		***16.29 (0.50)***		***12.79 (0.33)***	
Development time (days)	Immature	14	*63.68 (10.63)*	*49.73 (4.63)*	*31.76 (2.44)*	*27.86 (1.25)*	*21.16 (1.07)*	*19.35 (0.60)*	*15.86 (0.63)*	*14.82 (0.40)*
Survival fraction	Egg	16	0.75 (0.10)	0.61 (0.10)	0.71 (0.06)	0.57 (0.06)	0.78 (0.05)	0.64 (0.06)	0.61 (0.07)	0.47 (0.08)
Survival fraction	Larva 1	2	***0.83 (0.03)***		***0.92 (0.01)***		***0.95 (0.02)***		***0.84(0.01)***	
Survival fraction	Larva 2	10	*0.92 (0.02)*	*0.95 (0.01)*	0.96 (0.01)	0.98 (0.01)	0.97 (0.01)	0.99 (0.01)	*0.95 (0.01)*	*0.98 (0.01)*
Survival fraction	Larva 3	7	1.00 (0.08)	0.99 (0.01)	1.00 (0.04)	1.00 (0.01)	0.97 (0.01)	1.00 (0.01)	*0.90 (0.05)*	*0.97 (0.01)*
Survival fraction	Larva 4	9	***0.90 (0.04)***		***1.00 (0.02)***		***0.96 (0.02)***		***1.00 (0.03)***	
Survival fraction	Pupa	10	***0.92 (0.03)***		***1.00 (0.02)***		***0.99 (0.02)***		***0.89 (0.02)***	
Survival fraction	Larva	3	***0.67 (0.03)***		***0.90 (0.01)***		***0.90 (0.01)***		***0.82 (0.01)***	
Survival fraction	Larva + Pupa	14	*0.55 (0.05)*	*0.63 (0.10)*	*0.82 (0.03)*	*0.90 (0.09)*	*0.83 (0.03)*	*0.91 (0.09)*	*0.74 (0.03)*	*0.82 (0.09)*
Survival fraction	Immature	14	***0.44 (0.04)***		***0.65 (0.02)***		***0.62 (0.02)***		***0.34 (0.02)***	
Pre-oviposition time (days)		17	NA	*33.88 (14.88)*	*21.66 (5.20)*	*12.33 (1.70)*	*7.55 (0.52)*	*7.53 (0.62)*	4.57 (0.32)	5.43 (0.35)
Longevity (days)		10	*99.72 (13.30)*	*123.88 (14.88)*	*85.01 (8.63)*	*109.17 (11.52)*	*70.29 (6.92)*	*94.45 (10.96)*	*55.58 (9.86)*	*79.74 13.54)*
Generation time (days)		14	NA	132.48 (46.22)	*62.50 15.77)*	*49.97 (5.77)*	28.15 (2.65)	30.79 (2.18)	18.16 (1.44)	22.25 (1.29)
Daily fecundity (day^{-1})		15	*2.97 (3.96)*	*26.93 (7.68)*	*16.79 (1.99)*	*29.48 (3.74)*	*22.86 (1.72)*	*24.27 (3.14)*	21.17 (3.24)	11.30 (5.67)

SE are calculated from the fixed parts of the mixed-effect models. Italicized values depict the cells where the invasive population performs better than the native population, i.e. smaller predicted mean development time, higher survival fraction, shorter pre-oviposition time, smaller generation time, longer adult lifetime, or higher daily fecundity. Numbers given in bold italic letter type indicated that origin was not included as a factor in any model in the set of most supported models (ΔAICc < 2); The column labelled #20 gives the number of models in the 20 models with origin included that have origin included as a factor

NA = not available, because the linear relation gave a negative rate

lower temperatures a shorter generation time and greater daily fecundity than did native populations. These differences hold for the mean values predicted by the 'best origin model', but confidence intervals from the fixed effect models overlap. Therefore, these differences are not significant and need to be interpreted with caution.

Discussion

The debate on whether invading populations in Europe and North America have different life history parameters than native populations in Asia can partly be settled. Our meta-analysis of a worldwide dataset consisting of 82 studies shows differences in life history characteristics between native and invasive populations. Individuals of invasive populations had a shorter pre-oviposition period and higher fecundity at low temperatures than those of native populations, and a greater longevity across all temperatures.

Below we first discuss our findings for the covariable temperature and each of the four factors and, where possible, we relate them to results of other studies. Next we interpret the outcomes to answer our main questions: does *H. axyridis* have different life history characteristics in the invasive range as compared to the native range and can these differences explain its invasion success?

The covariable temperature was included in all of the most parsimonious models, supporting the major effect of temperature on insect development (Logan et al. 1976). For the survival parameters, temperature was usually the only explanatory variable selected in the most parsimonious model.

The factor photoperiod was included as an explanatory variable in five of the most parsimonious models that cover development rate (including the pre-oviposition period). Synthesis of data in this meta-analysis does not reveal any consistent photoperiod effect on developmental rates or survival. The only study comparing the effect of 14 h period with 16–18 h photoperiod on development (Reznik and Vaghina 2011), likewise did not find an effect of photoperiod.

Food emerged as an explanatory variable in only four of the most parsimonious models: three models for adult parameters and one for survival. The estimated effects were not consistent. Several individual studies directly compared the effect of *Ephestia* and aphid diets but the results were inconsistent (e.g. Kögel et al. 2012; Nedvěd and Kalushkov 2012; Rodrigues et al. 2013). These inconsistencies were carried over into the meta-analysis. Almost no data were available for native *Ephestia*-fed populations, and half of the invasive *Ephestia*-fed populations were laboratory strains: food type effect was therefore confounded with origin and strain. We only contrasted '*Ephestia*'- and 'aphid'-diets, variation in diets of aphid species with different quality may partly explain the low explanatory power of food in our models. In an initial exploration we did not find any consistent effect across studies of aphid species as food.

Laboratory rearing may select for fast development, short longevity, and high fecundity (Tayeh et al. 2012). The effect of rearing was, however, not consistent amongst studies comparing reared and wild strains (e.g. Berkvens et al. 2008a, b; Turgeon et al. 2011). Seven of the most parsimonious models included the factor strain. The meta-analysis shows that reared populations have shorter longevity and in some cases faster development (larva and 'larva plus pupa' but only for temperatures higher than 22 °C), but egg development of reared strains was slower. Datasets from the literature are almost inevitably unbalanced because an overarching experimental design is lacking. The dataset used here was no exception: for invasive populations 48% of the data points originated from laboratory reared strains, compared with only 12% for the native populations (Supplementary Information 3). While such imbalances affect the ability to draw conclusions, the effect of strain in the analyses confirms the common notion that laboratory reared insects differ in life history parameters from wild insects.

The meta-analysis used data from studies under controlled conditions. Hence the resulting models are for controlled conditions. Data collected in field studies in which no temperature was measured, yielded data for development and adult parameters that were in the same range of the data used for the model fitting. Development data for larva, pupa, 'larva plus pupa' and pre-adult development (Sakurai et al. 1993) and longevities (Katsoyannos et al. 1997) were close to the fitted relationship, while fecundities (Bazzocchi et al. 2004) were lower than the fitted relationship. Thus, the models for development and adult parameters, could, with some caution, be used to interpret field situations.

As expected, survival was for all stages usually substantially lower in the field than in the laboratory. Only the values for egg survival were similar for field and lab studies. The results suggest that most variation in immature survival occurs in the egg stage, as those of the other separate stages did not vary (always more than 83% survival). However, in the field the larval stage explains most variation in survival, not the egg stage (Kindlmann et al. 2000; Osawa 1993). Larval mortality tends to be density-dependent (Osawa 1993). The larvae suffer from intraguild predation and cannibalism when prey density drops (Yasuda and Shinya 1997). There are various other explanations for variable mortality in the wild, such as (escape from) parasitism (Comont et al. 2014). The discrepancy between data on survival in the field and under laboratory conditions suggests that caution is needed when extrapolating laboratory data on survival to field circumstances.

Meta-analysis aims to synthesise data from many studies and reach overarching conclusions. One surprising overarching finding in this study is the lack of accordance in responses of development time to origin, which represents the breadth of findings and reflects the ambiguous effects of geographic origin reported in the literature. Most separate stage analyses indicate that natives develop faster, the pupal stage shows no effect, and the entire pre-adult development points towards faster development in invasive populations (Table 2). Different datasets underlie these opposing results of our analyses. The datasets of the separate stages and the entire pre-adult development have only small overlap: e.g. less than 5% of the data points is shared. This means that the models for the different response variables are based on different datasets, and these are apparently contradictory.

The shorter pre-oviposition period and higher fecundity at low temperatures, and a greater longevity across all temperatures may provide an advantage in the early stages of invasion, when population densities are low, because it speeds up population growth and may help overcome Allee effects that are associated with small population sizes (Hill et al. 2011). Our conclusion that invasive populations have a higher fecundity at low temperatures and live longer at all temperatures than native populations, is in line with Tayeh et al. (2015). Higher fecundity, shorter pre-oviposition period, and a greater longevity may, of course, not be the only causes for the invasion success of *H. axyridis*. Additional factors explaining the invasion success of *H. axyridis* in northern Europe are significantly higher survival during the winter (Raak-van den Berg et al. 2012b), higher immature survival (Raak-van den Berg 2014), higher fecundity, higher longevity, more generations per year (Roy et al. 2016), and dominance in intraguild predation when compared with native European species (Pell et al. 2008; Raak-van den Berg et al. 2012a). *Harmonia axyridis* is also better defended by chemical deterrents (Sloggett et al. 2011), its immune system (Firlej et al. 2012), its larval morphology with dorsal spines (Pell et al. 2008), and its greater ability to escape from attack (Hautier 2003) than native species. Also, it has a strong dispersal capacity. During its invasion of Europe it has spread at rates estimated between 100 and 200 km year^{-1} (Brown et al. 2011) and Lombaert et al. (2014) showed that several traits related to dispersal have evolved in less than a decade. Further, *H. axyridis* populations may have profited until now from lack of natural enemies (Roy et al. 2011) as it invaded without or with few of its native natural enemies, and/or the natural enemies in the invaded area are not (yet) effectively attacking the exotic species (Haelewaters et al. 2017; Raak-van den Berg et al. 2014). As is often the case, there is likely to be no single cause of the observed patterns, and the success of *H. axyridis* in the invaded areas may well be the consequence of a combined effect of the mentioned factors. However, our paper shows that the further unravelling of the causes of the high invasion success by this species should certainly include the study of the exact mechanisms leading to life-history differences between invasive and native populations.

The results of this meta-analysis could also be used to construct global maps of the expected yearly population growth of invasive and native *H. axyridis* in different climate zones. These would assist in assessing the potential range of establishment of the species (Guisan and Thuiller 2005; Poutsma et al. 2008) and could also help answering the question whether the invasive or the native population would perform better in different climates worldwide. Such mapping needs modelling of its population dynamics, but could take the results of this study to the next level, and complement studies on specific components of the life strategy of *H. axyridis* that affect its ecological niche, such as cannibalism (Tayeh et al. 2014), male reproductive success and female reproductive

investment (Laugier et al. 2013), and resistance to pathogens (Tayeh et al. 2012).

In conclusion, in this paper we have demonstrated that invasive populations of *H. axyridis* differ in some of their life history characteristics from the populations in its area of origin, which provides a starting point for further study into the possible mechanisms causing these differences. Such information will be crucial to predict future scenarios with respect to the invasion process of *H. axyridis*, especially in the light of ongoing climate change. The *H. axyridis* case may also serve as a model for other invasive species in this respect. If it is known how and how fast invasive populations respond to a novel environment by selection, this has profound consequences for risk assessment protocols.

Acknowledgements We would like to thank several people for contributions: all authors who provided raw data or further explanation on their data; D. Lucas Barbosa, K. Oku, C. Ponzio, Y.T. Qiu, S. Wang, M. Yajima, P. Zhang, and S. Zheng for help with translation of manuscripts; and S.W. Benedictus-van den Berg, C. van Boxel, and M.J. Raak for other support.

References

Barton K (2014) MuMIn: multi-model inference. R package version 1.12.1. http://CRAN.R-project.org/package=MuMIn

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Soft 67(1):1–48

Bazzocchi GG, Lanzoni A, Accinelli G, Burgio G (2004) Overwintering, phenology and fecundity of *Harmonia axyridis* in comparison with native coccinellid species in Italy. BioControl 49:245–260

Berkvens N, Bonte J, Berkvens D, Deforce K, Tirry L, De Clercq P (2008a) Pollen as an alternative food for *Harmonia axyridis*. BioControl 53:201–210

Berkvens N, Bonte J, Berkvens D, Tirry L, De Clercq P (2008b) Influence of diet and photoperiod on development and reproduction of European populations of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). BioControl 53:211–221

Blekhman AV, Goryacheva II, Zakharov IA (2010) Differentiation of *Harmonia axyridis* Pall. according to polymorphic morphological traits and variability of the mitochondrial COI gene. Moscow Univ Biol Sci Bull 65:174–176

Bolker BM (2008) Ecological models and data in R. Princeton University Press, Princeton

Brown PMJ (2013) A global invader: the worldwide distribution of *Harmonia axyridis* (Coleoptera: Coccinellidae). IOBC/WPRS Bulletin 94:51–60

Brown PMJ, Adriaens T, Bathon H, Cuppen J, Goldarazena A, Hagg T, Kenis M, Klausnitzer BEM, Kovar I, Loomans AJM, Majerus MEN, Nedvěd O, Pedersen J, Rabitsch W, Roy HE, Ternois V, Zakharov IA, Roy DB (2008) *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. BioControl 53:5–21

Brown PMJ, Thomas CE, Lombaert E, Jeffries DL, Estoup A, Lawson Handley L-J (2011) The global spread of *Harmonia axyridis* (Coleoptera: Coccinellidae): distribution, dispersal and routes of invasion. BioControl 56:623–641

Caswell H (2001) Matrix population models: construction, analysis and interpretation, 2nd edn. Sinauer Associates, Sunderland

Chapin JB, Brou VA (1991) *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). Proc Entomol Soc Wash 93:630–635

Comont RF, Purse BV, Phillips W, Kunin WE, Hanson M, Lewis OT, Harrington R, Shortall CR, Rondoni G, Roy HE (2014) Escape from parasitism by the invasive alien ladybird, *Harmonia axyridis*. Insect Conserv Diver 7:334–342

Cuppen J, Heijerman T, van Wielink PS, Loomans AJM (2004) Het Lieveheersbeestje *Harmonia axyridis* in Nederland: een aanwinst voor onze fauna of een ongewenste indringer (Coleoptera: Cocinellidae)? Ned Faun Med 20:1–12

De Wit CT, Goudriaan J (1978) Simulation of ecological processes. Pudoc, Wageningen

Evans EW, Soares AO, Yasuda H (2011) Invasions by ladybugs, ladybirds, and other predatory beetles. BioControl 56:597–611

Facon B, Hufbauer RA, Tayeh A, Loiseau A, Lombaert E, Vitalis R, Guillemaud T, Lundgren JG, Estoup A (2011) Inbreeding depression is purged in the invasive insect *Harmonia axyridis*. Curr Biol 21:424–427

Firlej A, Girard PA, Brehelin M, Coderre D, Boivin G (2012) Immune response of *Harmonia axyridis* (Coleoptera: Coccinellidae) supports the enemy release hypothesis in North America. Ann Entomol Soc Am 105:328–338

Glass GV (1976) Primary, secondary, and meta-analysis of research. Educ Res 5:3–8

Goetz DW (2008) *Harmonia axyridis* ladybug invasion and allergy. Allergy Asthma Proc 29:123–129

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009

Haelewaters D, Zhao SY, Clusella-Trullas S, Cottrell TE, De Kesel A, Fiedler L, Herz A, Hesketh H, Hui C, Kleespies RG, Losey JE, Minnaar IA, Murray KM, Nedvěd O, Pfliegler WP, Raak-van den Berg CL, Riddick EW, Shapiro-Ilan DI, Smyth RR, Steenberg T, van Wielink PS, Viglášová S, Zhao Z, Ceryngier P, Roy HE (2017) Parasites of *Harmonia axyridis*: current research and perspectives. BioControl. doi:10.1007/s10526-016-9766-8

Hautier L (2003) Impacts sur l'entomofaune indigène d'une coccinelle exotique utilisée en lutte biologique. Université Libre de Bruxelles, MSc

Hilborn R, Mangel M (1997) The ecological detective: confronting models with data. Princeton University Press, Princeton

Hill JK, Griffiths HM, Thomas CD (2011) Climate change and evolutionary adaptations at species' range margins. Annu Rev Entomol 56:143–159

Katsoyannos P, Kontodimas DC, Stathas GJ, Tsartsalis CT (1997) Establishment of *Harmonia axyridis* on citrus and some data on its phenology in Greece. Phytoparasitica 25:183–191

Kenis M, Roy HE, Zindel R, Majerus MEN (2008) Current and potential management strategies against *Harmonia axyridis*. BioControl 53:235–252

Kindlmann P, Yasuda H, Sato S, Shinya K (2000) Key life stages of two predatory ladybird species (Coleoptera: Coccinellidae). Eur J Entomol 97:495–499

Kögel S (2012) Risikoabschätzung von *Harmonia axyridis*, dem Asiatischen marienkäfer, für den Deutschen obst-und weinbau. Julius Kühn-Institut

Kögel S, Eben A, Hoffmann C, Gross J (2012) Influence of diet on fecundity, immune defense and content of 2-isopropyl-3-methoxypyrazine in *Harmonia axyridis* Pallas. J Chem Ecol 38:854–864

Koricheva J, Gurevitch J, Mengersen K (2013) Handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton

Laugier GJM, Le Moguedec G, Tayeh A, Loiseau A, Osawa N, Estoup A, Facon B (2013) Increase in male reproductive success and female reproductive investment in invasive populations of the harlequin ladybird *Harmonia axyridis*. PLoS ONE 8(10):e77083

Li K, Chen X, Wang H (1992) New discovery of feeding habitats of some ladybirds. Shaanxi For Sci Technol 2:84–86

Logan JA, Wollkind DJ, Hoyt SC, Tanigoshi LK (1976) An analytic model for description of temperature dependent rate phenomena in arthropods. Environ Entomol 5:1133–1140

Lombaert E, Guillemaud T, Cornuet JM, Malausa T, Facon B, Estoup A (2010) Bridgehead effect in the worldwide invasion of the biocontrol harlequin ladybird. PLoS ONE 5(3):e9743

Lombaert E, Guillemaud T, Thomas CE, Lawson Handley L-J, Li J, Wang S, Pang H, Goryacheva I, Zakharov IA, Jousselin E, Poland RL, Migeon A, van Lenteren J, De Clercq P, Berkvens N, Jones W, Estoup A (2011) Inferring the origin of populations introduced from a genetically structured native range by approximate Bayesian computation: case study of the invasive ladybird *Harmonia axyridis*. Mol Ecol 20:4654–4670

Lombaert E, Estoup A, Facon B, Joubard B, Gregoire JC, Jannin A, Blin A, Guillemaud T (2014) Rapid increase in dispersal during range expansion in the invasive ladybird *Harmonia axyridis*. J Evol Biol 27:508–517

Majerus M, Strawson V, Roy H (2006) The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in Britain. Ecol Entomol 31:207–215

Nedvěd O, Kalushkov PK (2012) Effect of air humidity on sex ratio and development of ladybird *Harmonia axyridis* (Coleoptera: Coccinellidae). Psyche 2012:5

Obrycki JJ, Tauber MJ (1982) Thermal requirements for development of *Hippodamia convergens* (Coleoptera, Coccinellidae). Ann Entomol Soc Am 75:678–683

Osawa N (1993) Population field studies of the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): life tables and key factor analysis. Res Popul Ecol 35:335–348

Pell JK, Baverstock J, Roy HE, Ware RL, Majerus MEN (2008) Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives. BioControl 53:147–168

Phoofolo MW, Obrycki JJ (1995) Comparative life-history studies of Nearctic and Palearctic populations of *Coccinella septempunctata* (Coleoptera: Coccinellidae). Environ Entomol 24:581–587

Poutsma J, Loomans AJM, Aukema B, Heijerman T (2008) Predicting the potential geographical distribution of the harlequin ladybird, *Harmonia axyridis*, using the CLIMEX model. BioControl 53:103–125

Raak-van den Berg CL (2014) *Harmonia axyridis*: how to explain its invasive success in Europe? PhD Thesis. Wageningen University, Wageningen. http://library.wur.nl/WebQuery/clc/2068101

Raak-van den Berg CL, de Lange HJ, van Lenteren J (2012a) Intraguild predation behaviour of ladybirds in semi-field experiments explains invasion success of *Harmonia axyridis*. PLoS ONE 7(7):e40681

Raak-van den Berg CL, Stam JM, de Jong PW, Hemerik L, van Lenteren J (2012b) Winter survival of *Harmonia axyridis* in The Netherlands. Biol Control 60:68–76

Raak-van den Berg CL, van Wielink P, De Jong PW, Gort G, Haelewaters D, Helder J, van Lenteren JC (2014) Invasive alien species under attack: natural enemies of *Harmonia axyridis* in the Netherlands. BioControl 59:229–240

Reznik SY, Vaghina NP (2011) Photoperiodic control of development and reproduction in *Harmonia axyridis* (Coleoptera: Coccinellidae). Eur J Entomol 108:385–390

Rodrigues ARdS, Spindola AF, Oliveira JEdM, Torres JB (2013) Dietary effects upon biological performance and lambda-cyhalothrin susceptibility in the multicolored Asian lady beetle, *Harmonia axyridis*. Phytoparasitica 41:285–294

Roy HE, Rhule E, Harding S, Lawson Handley L-J, Poland RL, Riddick EW, Steenberg T (2011) Living with the enemy: parasites and pathogens of the ladybird *Harmonia axyridis*. BioControl 56:663–679

Roy HE, Brown PMJ, Adriaens T, Berkvens N, Borges I, Clusella-Trullas S, Comont RF, De Clercq P, Eschen R, Estoup A, Evans EW, Facon B, Gardiner MM, Gil A, Grez AA, Guillemaud T, Haelewaters D, Herz A, Honek A, Howe AG, Hui C, Hutchison WD, Kenis M, Koch RL, Kulfan J, Lawson Handley L, Lombaert E, Loomans A, Losey J, Lukashuk AO, Maes D, Magro A, Murray KM, Martin GS, Martinkova Z, Minnaar IA, Nedvěd O, Orlova-Bienkowskaja MJ, Osawa N, Rabitsch W, Ravn HP, Rondoni G, Rorke SL, Ryndevich SK, Saethre M-G, Sloggett JJ, Soares AO, Stals R, Tinsley MC, Vandereycken A, van Wielink P,

Viglášová S, Zach P, Zakharov IA, Zaviezo T, Zhao Z (2016) The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and ecology. Biol Invasions 18:997–1044

Sakurai H, Kumada Y, Takeda S (1993) Seasonal prevalence and hibernating diapause behaviour in the lady beetle, *Harmonia axyridis*. Res Bull Fac Agric Gifu Univ 58:51–55

Sloggett JJ (2012) *Harmonia axyridis* invasions: deducing evolutionary causes and consequences. Entomol Sci 15:261–273

Sloggett JJ, Magro A, Verheggen FJ, Hemptinne JL, Hutchison WD, Riddick EW (2011) The chemical ecology of *Harmonia axyridis*. BioControl 56:643–661

Tayeh A, Estoup A, Laugier G, Loiseau A, Turgeon J, Toepfer S, Facon B (2012) Evolution in biocontrol strains: insight from the harlequin ladybird *Harmonia axyridis*. Evol Appl 5:481–488

Tayeh A, Estoup A, Lombaert E, Guillemaud T, Kirichenko N, Lawson-Handley L, De Clercq P, Facon B (2014) Cannibalism in invasive, native and biocontrol populations of the harlequin ladybird. BMC Evol Biol 14:15

Tayeh A, Hufbauer RA, Estoup A, Ravigne V, Frachon L, Facon B (2015) Biological invasion and biological control select for different life histories. Nat Commun. doi:10.1038/ncomms8268

Turgeon J, Tayeh A, Facon B, Lombaert E, De Clercq P, Berkvens N, Lundgren JG, Estoup A (2011) Experimental evidence for the phenotypic impact of admixture between wild and biocontrol Asian ladybird (*Harmonia axyridis*) involved in the European invasion. J Evol Biol 24:1044–1052

van Lenteren JC (2012) The state of commercial augmentative biological control: plenty of natural enemies, but a frustrating lack of uptake. BioControl 57:1–20

Wang S, Michaud JP, Tan XL, Zhang F, Guo XJ (2011) The aggregation behavior of *Harmonia axyridis* in its native range in Northeast China. BioControl 56:193–206

Whitney KD, Gabler CA (2008) Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. Divers Distrib 14:569–580

Yasuda H, Shinya K (1997) Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. Entomophaga 42:153–163

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

C. Lidwien Raak-van den Berg performed this study as part of her PhD project focussing on life history characteristics of *Harmonia axyridis* and the beetle's establishment and spread in Europe.

Lia Hemerik is a mathematical biologist whose current work focuses on statistical and mathematical modelling of population dynamical processes, behavioural ecology, conservation biology, aquatic ecology and soil biology.

Wopke van der Werf studies ecological processes in agricultural systems from field to landscape scale to contribute to understanding and strengthening of ecosystem services in agricultural systems.

Peter W. de Jong studies the adaptation of insects in a multitrophic context, focussing on the mechanisms underlying the geographical and temporal distribution patterns of adaptations.

Joop C. van Lenteren works on behavioural ecology and population dynamics of parasitoids, theoretical and practical aspects of biological control, IPM and sustainable crop production.